Complex learning in *Octopus bimaculoides*

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Abstract. In order to investigate complex learning in *Octopus bimaculoides* (Pickford and McConnaughey), I presented subjects with a series of combinations of mollusc shells. Combinations consisted of two shells of one type and an odd shell of another type. The shells were suspended in the octopuses' home tanks, and the animals were rewarded with food for correctly grabbing the odd shell. Associative learning was demonstrated by the subjects' eventual mastery (70 - 100% success rates) of each combination in a series (A+ B− B−), (C+ D− D−) ... By mastery of new combinations of the same stimuli, (A+ D− D−), (C+ B− B−) ,..., subjects demonstrated transfer of learning. Learning improved across successive combinations, evidence for learning set formation. However, because octopuses did not learn to choose the odd stimulus when trained only with non-repeating combinations, no evidence indicated that the octopuses formed the relative class concept of oddity.

The demonstration of complex learning in cephalopods could provide important insight into the evolution of cognition. Most research on complex learning has focused on higher vertebrates. However, an ecological approach suggests that complex learning could evolve whenever it was adaptively advantageous (Shettleworth, 1984). Several investigations have suggested a connection between complex learning abilities and sociality (see Humphrey, 1976; Essock-Vitale and Seyfarth, 1986). Wells (1978) has argued, however, that because the predominantly solitary octopuses have no obvious means of self defense and live in a highly competitive environment, they also could show complex learning. The experiments reported here test this proposal.

I presented *Octopus bimaculoides* (Pickford and McConnaughey) with three objects, two alike and one different, and rewarded them with small pieces of squid if they grabbed the odd one. Using this methodology, I could pose a series of problems differing in the complexity of learning required for successful mastery.

The first question was, could the octopuses learn to choose a particular shell, in repeated presentations of the same combination? Simple associative learning of this sort has previously been demonstrated with *Octopus vulgaris* (Cuvier) (Wells, 1978).

The second question was, could the octopuses still pick the correct shell if known shells were arranged into new combinations? Positive results would show transfer of learned response tendencies.

Thirdly, as the animals gained experience in learning shell combinations, would they improve at learning new but similar tasks? An ability for learning to learn, or developing a learning set, has not been shown previously in an invertebrate, although the related task of learning reversals has (Mackintosh, 1965; Morrow and Smithson, 1969).

Lastly, could the octopuses eventually generalize and immediately choose the odd shell when presented with new combinations? Generalization has been shown in tactile discriminations for *Octopus vulgaris* (Wells and Young, 1970). This task is particulary significant because oddity is an abstract concept, defined only in relationship to other objects and not by any attribute of the object itself. So far, only higher invertebrates have shown evidence of forming such relative class concepts (Thomas, 1980; Lombardi *et al.*, 1984; Thomas and Noble, 1988).

METHODS

EXPERIMENT I

Subjects were three wild caught adults of undetermined sex which had been living in the laboratory a full six months before experiments began. In the laboratory, they were nocturnal and not easy to clock-shift. Therefore, experiments were performed at night under red light.

The octopuses were trained initially to take small pieces of frozen squid from a rod and, later, to grab a single plastic triangle or square on the end of a rod to get a food reward. On days when they were unsuccessful with discrimination tasks, I fed them after trials using the rod alone, up to their minimum daily intake.

Trials consisted of presenting three stimuli, two alike and one different. Six different combinations were used (Appendix 1). The combinations presented were composed of mollusc shells varying in color, texure, and shape, except for combinations four and five, which consisted of plastic shapes which varied in both texture and shape.

I suspended the stimuli on nylon monofilament in the

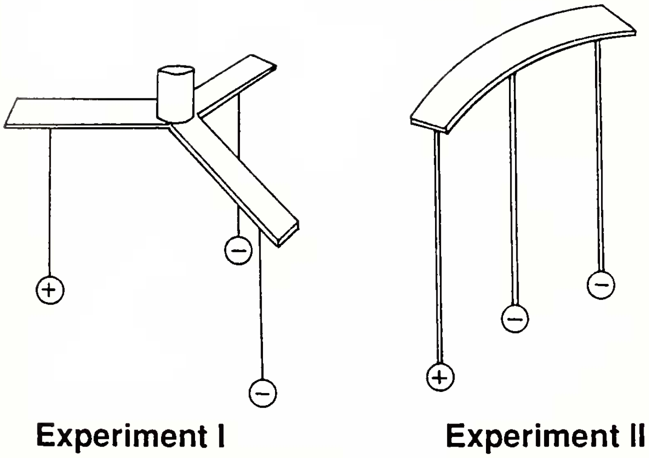

Fig. 1. Apparatus for presenting combinations of shells. Location of the odd, positive stimulus (+) was determined randomly. In Experiment I, the shells were suspended on monofilament; in Experiment II, they were attached to acrylic rods.

octopuses' tanks (Fig. 1). The location of the odd object was determined randomly, with the constraint that in half of the presentations it was in the front half of the tank, and in half it was in the back. A subject was then given two minutes in which to grab one of the stimuli. Responses were usually immediate. A correct response was promptly rewarded with a small piece of squid. I gave each subject eight trials per learning session, ten to fifteen minutes apart, with two learning sessions per day, 11 sessions per week.

In Experiment I, each of the six combinations was presented for 11 sessions or until all subjects reached a success rate of greater than 50% for three successive sessions. The second combination was cut short because one of the shells was shattered by a particularly vigorous grab. Octopuses were then retested for two or three sessions with each familiar combination. They were then each given an equal number of presentations with three of eight arbitrarily chosen new combinations of the same, familiar stimuli. Positive, rewarded shells remained positive and negative, unrewarded shells remained negative; however, the particular combinations of positive and negative stimuli were new.

Experiment I ran for a total of 119 sessions across 12 weeks. Response rates averaged 43% for the three octopuses. For each octopus, sessions with fewer than two grabs were eliminated from the study.

EXPERIMENT II

Subjects were three freshly caught *Octopus bimaculoides*, just reaching sexual maturity, one female and two males. Initial training was carried out as described above. Trials consisted of presentation of three stimuli, two alike and one different, as before. All stimuli used were mollusc shells (Appendix 2). Shells were presented in a line (Fig. 1) to correct for the location bias found in Experiment I. I gave the octopuses ten trials each learning session, spaced five to ten minutes apart, with one session per day, six days per week.

In this experiment, every combination presented to a subject (each trial) was novel. Sixty pairs of shells were used, with every type of shell presented both as a positively rewarded odd shell and as a negative pair, in order to control for the possibility that subjects had attended to some attribute other than oddity. Each type of shell was therefore seen by the octopuses only twice within each week: once as a positive single shell, and once as a negative pair of shells. The only way to solve this problem successfully would be to employ the relative class concept of oddity.

Combinations of shells were determined randomly with the constraint that positive odd shells differed from the negative pair by two of the three features of color, texture, or type (bivalve or gastropod) (Appendix 2). Orders of presentation and locations of the odd shells were randomized.

Simple reinforcement trials were given at the beginning and end of each training session and randomly interspersed among the oddity discrimination problems. These trials consisted of presenting the octopus with the single plastic triangle or square used in initial training. Octopuses were rewarded for grabbing the shape (no choice or discrimination was involved). Response rates in discrimination tasks were 89%. To reduce any inadvertent cuing, beginning with the second week of trials a gauze curtain was draped between the experimenter and the octopuses, with red lights only on the octopuses' side.

RESULTS

EXPERIMENT I

Performances of the three octopuses were statistically indistinguishable (contingency table for three subjects versus correct or incorrect response: $\chi^2 = 0.694$, d.f. = 2, $P > 0.70$). Results were therefore pooled.

Octopuses showed a strong bias towards objects in the front of the tank in the first experiment ($\chi^2 = 107.15$, d.f. = 1, $P < 0.01$); subjects grabbed front stimuli more frequently and less accurately. Response rates were low and not related to success rates (Figs. 2, 3).

Could the octopuses learn to choose correctly one object out of a combination with repeated presentations? Success rates for the first combination, in terms of correct choices as a percentage of total grabs (Fig. 2), showed clearly that the combination was learned and retained. Despite the small sample size and wide variability in performances, learning curves for the first 11 sessions of all six combinations (Fig. 3) demonstrated that the octopuses were able to learn to choose the correct object consistently.

Could they still choose the correct shell if known shells were recombined in new ways? This task required the ability

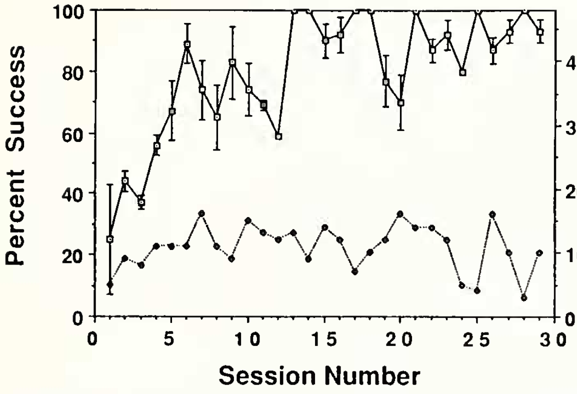

Fig. 2. Mean success rates (squares) (number of correct grabs as percentage of total grabs) with standard errors and total number of grabs (diamonds) across sessions, for the three octopuses on the first discrimination combination.

to remember five (combination two had been broken) simultaneous discriminations, or positive or negative attributes of at least five of the ten different stimuli. Their high success rate with the familiar arrangements shows good retention over this time period, and also shows that five simultaneous discriminations can be mastered by these octopuses. That they performed equally well on the original and new combinations (t = 1.01, d.f. = 26, P > 0.20) is evidence of transfer of learning (Fig. 4); they could use the learned information about member shells of a combination in a new context.

Could the octopuses improve at the task of learning new combinations? Variability was too high and sample sizes too small for comparisons to be made among slopes and intercepts of the six learning curves in the series. However, performances on days one and five (Fig. 5) (or for combination two, the last two completed learning sessions) across the six sequential combinations showed a trend toward improvement in first-day performances. For the sixth combination, a second observer was present on the first day and not on the fifth, a difference that could have affected performances. A paired comparisons test on all six combinations for the two days showed significant effects for both day and combination (days, F = 18.98, d.f. = 1,5, P < 0.01; combinations, F = 10.81, d.f. = 5,5, P < 0.025). The octopuses thus both learned the individual combinations and improved across the series. Sample sizes were too small to control for any effects of shells (combinations 1-3, and 6) versus plastic objects (combinations 4-5).

The last question was, could the octopuses generalize and choose the odd object after learning a number of different combinations? Their very high success rates on day one for the later combinations suggested that they might have formed the relative class concept of oddity. Experiment II was undertaken to explore this possibility further.

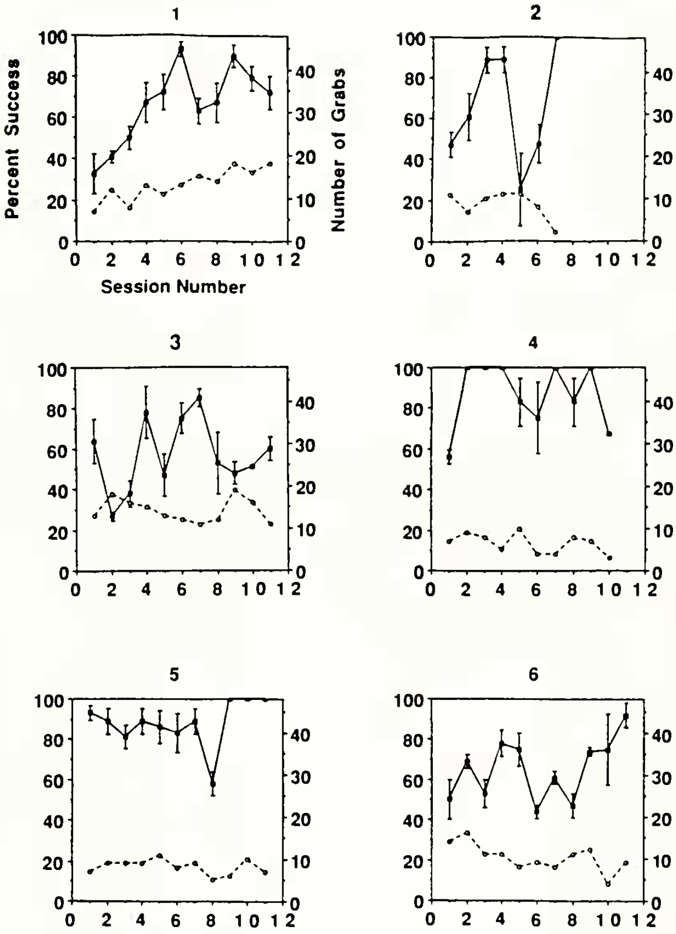

Fig. 3. Mean success rates and standard errors for each of the six combinations (n=3). Dotted lines indicate the total number of responses. Note the above-random performance on all combinations, despite wide variation.

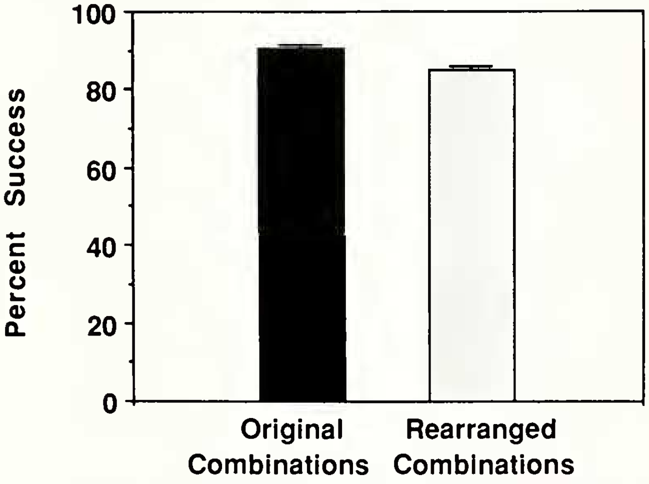

Fig. 4. Mean success rates and standard errors for the three octopuses with five original combinations (n=13) and with eight new combinations of familiar stimuli (n=15).

EXPERIMENT II

Performances of the three octopuses were once again statistically indistinguishable (contingency table for three subjects versus correct or incorrect response: $\chi^2 = 0.132$, d.f. $= 2$, $P > 0.90$). Results were therefore pooled.

The performance of the octopuses in choosing the odd object showed no clear improvement over time (Fig. 6). When mean success rates are separated by week (or by natural breaks), performances appeared slightly, but not significantly, better than completely random (33%). The means by week were 38, 36, 36, 47, and 40% (n=18).

The periodicity found in this learning curve (Fig. 6) was unexpected. It did not correspond to the six session work weeks and was not evident in all three individuals' performances (Fig. 7).

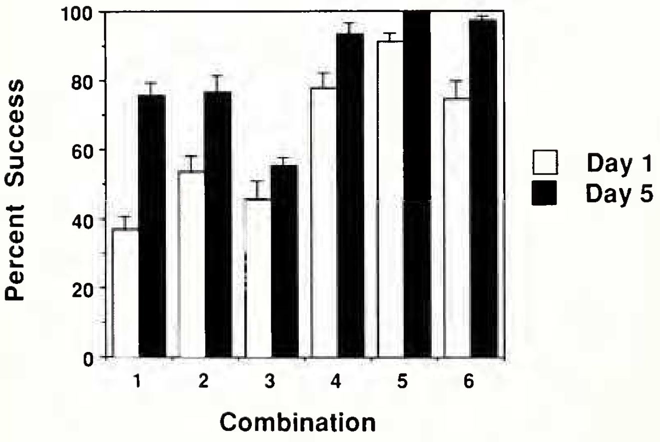

Fig. 5. Mean success rates and standard errors for days one and five for each of the six sequential combinations.

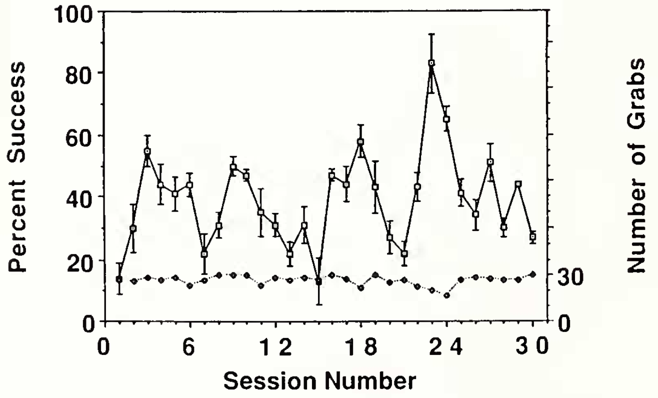

Fig. 6. Mean success rates (squares) with standard errors (n=3) and total numbers of responses (diamonds) across sessions in Experiment II when every combination presented was novel.

DISCUSSION

Octopus bimaculoides, a small octopus from the southern California coast, is a solitary, nocturnal predator, feeding primarily on gastropods but also on bivalves, polychaete worms, fishes, and crabs (Forsythe *et al.*, 1984). It lives in dens or burrows and interacts rarely with other octopuses (Lang, 1990). Generations do not overlap, which precludes the level of social learning available to even the most solitary of mammals. Laboratory-reared octopuses have the reputation of being slower to learn than those caught wild, perhaps an indication that learning takes place normally in their environment.

The particular tasks in these experiments do not relate directly to any activities known to be performed in the wild. However, they are comparable to experimental tests used to assess cognitive abilities in a wide range of species (Thomas, 1980).

In Experiment I, the octopuses' mastery of the simple task of learning to choose a particular shell after repeated presentations of the same combination is clear evidence of associative learning. This result is consistent with findings for *Octopus vulgaris* (Wells, 1978) as well as other invertebrates (Corning *et al.*, 1976).

Transfer of learning was also evident from performances on new combinations of familiar stimuli, an indication that their learning was not tightly dependent on context. Whether they based their choices on learned positive identities, learned negative identities, or both, cannot be determined from this experiment. However, response patterns suggest that they did in fact learn both. The octopuses normally sat in one of the top front corners of the tanks during trials. During the first experiment, they quickly stopped swimming to the far side of the tank (approximately an extra 20 cm) in order to grab the far stimulus. Therefore, they had to decide not only which stimulus to grab, but which stimuli not to grab, since the two nearby shells might both be negatives. They were highly successful at learning these discriminations, an indication that they had, in fact, learned both positive and negative shell identities.

That learning was retained over time was shown in the transfer of learning trials. The octopuses' success rate with the first combination was 80%, when retested after five weeks of experience with other combinations. Informal observations suggest that these animals might show retention even for months.

Learning set formation, or learning to learn, implies that something beyond recognition of objects has been learned. It could be only to attend carefully to relevant stimuli. Or, it could involve remembering previous choices and outcomes so as to arrive more quickly at correct solutions. Although learning set formation has not been shown previously in invertebrates, the related task of learning reversals has been mastered by isopods (Morrow and Smithson, 1969) and

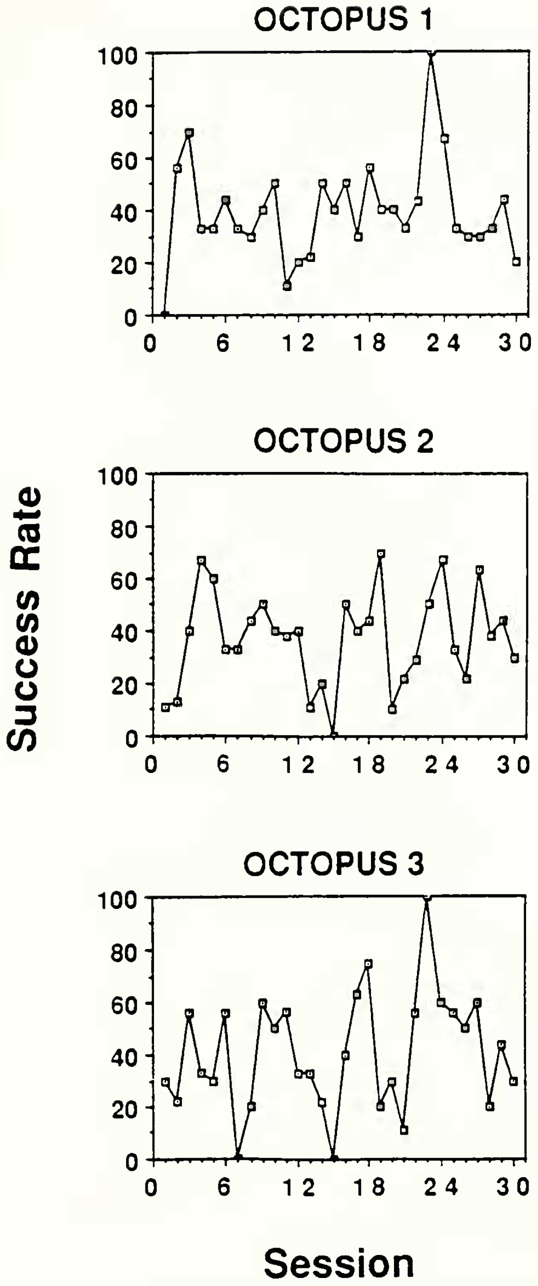

Fig. 7. Mean success rates across sessions for each subject in Experiment II when every combination presented was novel.

by octopuses (Mackintosh, 1965). Now that learning set formation has been indicated in octopuses, experiments with a longer learning set (many more combinations) could make comparisons with vertebrate species possible.

The results from the Experiment II showed no evidence of octopuses learning the concept of oddity. The results were surprising, after the octopuses' promising first day performances towards the end of the learning set. It is possible that more time was needed; the first experiment took place across three months as opposed to only five weeks for the second experiment. Or, it could be that repeated learning of exemplars, as in the first experiment, could succeed where the repeated novel presentations did not. It also could be that the curtain used during the second experiment prevented cuing that biased the first experiment.

The apparent periodicity in the learning curve for this experiment has no clear explanation. The learning curves for the first experiment also showed temporal variability in performance, especially prior to mastery of the task, but no apparent periodicities. Sanders (1977) has documented octopus learning curves to be multiphasic, corresponding to possible transitions between short- and long-term memory processes. However, his experiments were examining retention of a learned task across hours as opposed to performances of new tasks across days. I expect that the pattern observed in this experiment was simply an artifact of the small sample size and short duration of the experiment.

There were a number of problems in Experiment I. First, response rates were low, perhaps because, with so many trials each day, the smallest practical food rewards still added up to more than their normal daily intake levels. Another related explanation is that older, laboratory-habituated animals seem to have smaller appetites and to be less responsive in general. Second, choices during the first trial of each training session were significantly less accurate, as compared to subsequent trials ($\chi^2 = 22.884$, d.f. $= 7$, $P < 0.01$). Results from this experiment were therefore conservative. Third, animals were significantly more likely to grab stimuli in the front half of the tank. The experimental design was balanced, however, for front and back placement of the odd object. These three problems appeared to be addressed successfully in Experiment II by switching to a linear presentation, providing simple reinforcement trials at the beginning of each session, limiting trials to ten per day, and using younger, freshly caught animals.

Clearly, octopuses are capable of some forms of complex learning. While it remains to be seen if these octopuses can master a relative class concept such as oddity, these exploratory experiments suggest that the abilities underlying the formation of a learning set have evolved in an invertebrate, as well as in vertebrates (Pearce, 1987). They provide further evidence for convergences in function despite divergences in physiology between invertebrates and vertebrates (Packard, 1972; Corning *et al.*, 1976).

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APPENDIX 1

Combinations in Experiment I

Combination 1: *Noetia ponderosa* (Say) (+), *Anomia simplex* Orbigny (−).

Combination 2: *Anomia simplex* Orbigny (+), *Chione cancellata* (Linné) (−).

Combination 3: *Aequipecten gibbus* (Linné) (+), *Mercenaria mercenaria* (Linné) (−).

Combination 4: White square plastic grid (3 x 3 x 1 cm) (+), white square flat plastic chip (3 x 4 x .4 cm) (−).

Combination 5: white PVC adaptor fitting, threaded by slip, six-sided middle section (2.9 x 4 cm) (+), white PVC pipe section (4.1 cm diam. x 1.6 cm width) (−).

Combination 6: *Crassostrea virginica* (Gmelin) (+), *Busycon contrarium* (Conrad) (−).

APPENDIX 2

Combinations in Experiment II

Trials in Experiment II consisted of presenting combinations of three shells, two of one species and one of another. Species were chosen randomly with the constraint that the two types of shells of a combination must differ on two of three features (texture: 1=smooth, 2=ridged, 3=pointed; type: 1=gastropod, 2=bivalve or slipper; color: 1=light, 2=dark, 3=patterned).

Species included were: *Aequipectin gibbus* (Linné) (2,2,3); *Amphidromus entobaptus* (Dohrn) (1,1,1); *Anadara brasiliana* (Lamarck) (2,2,1); *A. ovalis* (Bruguiere) (2,2,1); *A. ovalis* (Brugiere) (2,2,1); *Anomia simplex* Orbigny (1,2,1); *A. simplex* (1,2,1); *A. simplex* (1,2,2); *Argopecten* sp. (2,2,1); *A.* sp. (2,2,2); *A.* sp. (3,2,3); *A.* sp. (2,2,3); *Arca zebra* Swainson (2,2,3); *Architectonia nobilis* Roding (2,1,3); *Babylonia areolata* (Link) (1,1,3); *Bursa* sp. (3,1,3); *Chicoreus cichoreum* (Gmelin) (3,1,3); *Chione cancellata* (Linné) (2,2,3); *C. cancellata* (2,2,1); *C. cancellata* (2,2,1); *C. cancellata* (2,2,1); *C. paphia Linné* (2,2,3); *Conus pulcher* Lightfoot (1,1,1); *Crassostrea virginica* (Gmelin) (1,2,2); *C. virginica* (2,2,1); *C. virginica* (1,2,2); *C. virginica* (2,2,1); *Crepidula fornicata* (Linné) (1,2,1); *C. fornicata* (1,2,1); *C. fornicata* (1,2,2); *C. fornicata* (1,2,1); *Dodinia discus* (Reeve) (1,2,1); *Ficus subintermedia* (Orbigny) (1,1,1); *Geukensia demissa* (Dillwyn) (2,2,2); *Helicostyla* sp. (1,1,3); *Haliotis asinia* Linné(1,2,2); *Liguus virineus* (Linné) (2,1,3); *Lucina pectinata* (Gmelin) (2,2,1); *Marisa cronuarietis* (Linné) (1,1,3); *Melongena corona* Gmelin (3,1,3); *Mercenaria mercenaria* (Linné) (1,2,1); *Murex fulvescens* Sowerby (3,1,1); *Natica* sp. (1,1,1); *N. stellata* Chenu (1,1,1); *Noetia ponderosa* (Say) (2,2,1); *N. ponderosa* (2,2,1); *N. ponderosa* (2,2,2); *Oliva sayana* Ravenel (1,1,1); *O. servicea* Roding (1,1,3); *Phalium granulatum* (Born) (1,1,3); *Pitar morrhuana* (Linsley) (1,2,2); *Pleuroplaca* sp. cf. *glabra* (Dunker) (2,1,1); *Sinum perspectiuum* (Say) (1,2,1); *Sisula solidissima* (Dillwyn) (1,2,1); *Tagelus plebius* (Lightfoot) (1,2,1); *Tectarius* cf. *Coronatus valenciennes* Gmelin (3,1,3); *Telescopium telescopium* (Linné) (1,1,2); *Tellina alternata* Say (2,2,1); *Trachycardium egmontium* (Shuttleworth) (2,2,1); *T. egmontium* (2,2,2); *Turbo* sp. (1,1,1); *T.* sp. cf. *petholatus* Linné (1,1,2); *Turritella* sp. (2,1,3); *Vexillum rugosum* (Gmelin) (2,1,3).